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REVIEW PAPER

Integrating species distribution modelling into decision-making to inform conservation actions

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Abstract Species distribution models (SDMs) have been widely tagged as valuable tools in a variety of conservation assessments to address pressing conservation problems. However, these solutions could be hampered by difficulties to overcome the knowledge-action boundary between conservation and modelling practice. These difficulties have been well typified in the ecological modelling sphere, but a specific conceptual framework on how to bridge this gap is still lacking. This work reports successful examples on how to use SDMs to identify the most favourable habitats for implementing conservation management actions. We use these examples to discuss about the three main topics that deserve special attention to help enhance information flow between practitioners and modellers: the decision context, the modelling framework and the spatial products. Finally, we suggest some practical solutions to improve applications of effective conservation action on the ground. We emphasize the importance of matching modelling goals and decision targets by a close collaboration of modellers with decision makers and species experts. Moreover, we highlight the key role of clear and useful spatial products to provide relevant and timely

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feedback to increase understanding and promote utilisation by conservation practitioners, and to inform and involve targeted audiences.

Keywords Conservation management · Environmental payments · Habitat corridor · Implementation gap · Knowledge-action boundary · Risk assessments · Species distribution models

Introduction

The geographical distribution of species is a key question for biodiversity conservation, since it underlies the context in which conservation actions are to be planned or implemented. Accordingly, the availability of robust and reliable information on species distribution and distribution changes has been one of the cornerstones of biodiversity conservation science (Pullin 2002). Predictions from spatial models relating species occurrences or abundance to environmental data offer a valuable source of information on species distributions with strong potential for prioritizing conservation and management actions (Ferrier et al. 2002; Jetz et al. 2012). The wide range uses of species distribution modelling have boosted the development of applications in different ecology and biogeography research areas, including biodiversity conservation (Anderson and Martinez-Meyer 2004; Rodriguez et al. 2007; Guisan et al. 2013). This interest has been recently amplified by the increasing availability of species distribution data and the development of GIS tools to handle and analyse spatial information (Jetz et al. 2012).

Models are key tools to explore hypotheses and have the potential to evaluate solutions within complex systems. Ecological models can therefore become useful tools for practitioners seeking for better decisions in conservation policy and practice. But often the context in which the decisions are to be made is ignored (Schmolke et al. 2010) when models objectives are defined, failing to adequately address practical context-dependent issues (e.g. urgent need of action, lack of financial resources, bureaucratic restrictions within agencies) so critical to achieve effective implementation of conservation actions. The difficulty in translating research outcomes into conservation action has been tagged as the “implementation crisis” (e.g. Knight et al. 2006; Prendergast et al. 1999; Salafsky et al. 2002), and it is contextualized in a broader issue of turning knowledge from applied research into action known as the “knowing-doing gap” (Pfeffer and Sutton 1999). Conservation practice suffers from this gap both at the planning and management levels. The “assessment-planning gap” concerns to the difficulty to achieve reliable conservation planning strategies by means of impracticable scientific knowledge and without true involvement of relevant agencies and stakeholders in the planning process. Similar obstacles hamper the translation of planning outcomes into conservation management action on the ground, i.e. the “planning-action gap” (Knight et al. 2006). Many authors have pointed out engagement impediments from both researchers and decision makers as the major pitfall to overcome this gap. Some of these impediments are, for instance, differences on funding sources, work planning, career aspirations or reward structures (Cook et al. 2013; Guisan et al. 2013). These differences draw a knowledge-action boundary faintly porous to information flow across the research and management realms. Information flows between two realms is further limited by misconceptions from both academic scientists and conservation practitioners about the context of the conservation

management problems (Knight et al. 2008; Laurance et al. 2012), and about the utility (or even the existence) of valuable research insights (Pullin et al. 2004; Addison et al. 2013). Communication, translation and mediation between scientists and practitioners have been pointed out as necessary functions to better bridge this boundary (Cash et al. 2003; Schmolke et al. 2010). As suggested by Soberón (2004) and Guisan et al. (2013), these functions would be performed by 'translators' between scientists and decision makers, embodied by intermediate organizations, individuals, groups or consortia. These translators would reconcile the research/policy interface by clearly communicating useful scientific contributions and ensuring that researchers and decision makers are jointly involved in facing complex environmental problems (Guisan et al. 2013). However, this task is particularly challenging when translating ecological models into non-modeller audiences lacking technical understanding. This is important when adequate communication skills are not guaranteed by conventional scientific careers. Good modelling practices accompanied by standardized, brief and practical documentation has been acknowledged as a key tool to ensure understanding and acceptance of modelling outcomes in environmental decision support (Schmolke et al. 2010; Addison et al. 2013).

Species distribution models (SDMs) have been widely tagged as valuable tools in a variety of conservation assessments to address pressing conservation problems (Franklin 2009). Improved knowledge of species actual distribution provides useful ecological insights and strong predictive capabilities to inform species distribution and assess sampling strategies of rare and endangered species (e.g. de Siqueira et al. 2009; Guisan et al. 2006; Marcer et al. 2012; Pearson et al. 2007; Raxworthy et al. 2003; Thomas et al. 2004), to establish conservation priority areas and design nature reserve networks (e.g. Arcos et al. 2012; Fajardo et al. 2014; Hermoso et al. 2015; Pawar et al. 2007; Wintle et al. 2005), or to guide species recovery and ecological restoration efforts (e.g. Angelieri et al. 2016; Clavero and Hermoso 2015; Fei et al. 2012; Gastón and García-Viñas 2013). Furthermore, SDMs can be extrapolated to new geographic or temporal scenarios as a component, for instance, of invasive species risk assessments (e.g. Ficetola et al. 2007; Jiménez-Valverde et al. 2011; Roura-Pascual et al. 2007) and to forecast (or hind cast) potential impacts of climate change (e.g. Ficetola et al. 2010; Runge et al. 2016) or other environmental changes (e.g. Jetz et al. 2007; Martin et al. 2013; Regos et al. 2016; Vallecillo et al. 2009). However, most of these assessments published in peer-reviewed journals consist of scientific analyses which lack real-world conservation contexts of application (Rodriguez et al. 2007; Guisan et al. 2013). Far less scientific attention has been devoted to practical approaches for developing strategies that make effective use of SDMs through inclusive decision-making processes, to improve prospects for implementation and, ultimately, optimize conservation efforts (Knight et al. 2006; Addison et al. 2013; Guisan et al. 2013). We currently lack specific conceptual frameworks on how to bridge the gap between methodological developments in SDMs and practical use for effective conservation practice.

This work reports successful examples on how to translate SDMs to identify the most favourable habitats for implementing conservation management action within the framework of a regional conservation project jointly performed by researchers from a boundary organization, as 'translators', and the Catalan Biodiversity and Animal Protection Agency (hereinafter Wildlife Agency) staff. We discuss about the main topics identified to tackle real-world conservation applications, emphasizing the importance to match clearly modelling goals with decision targets based on an early and effective communication with decision makers and other key stakeholders. We also highlight the need of model documentation and spatial products to provide relevant and timely feedback for increase

understanding and promote utilisation by conservation practitioners, and also to inform and involve targeted audiences.

Moving from theory to application: conservation actions and informing SDMs

The weak feedback between practitioners and modellers is the main pitfall to boost applied research within conservation practice. Hence, the key issue when designing the information flow between conservation and modelling practice is to enhance communication channels, and better if they go beyond personal skills of the people involved. Transparent and practical modelling outcomes suited as comprehensive spatial products are potential keystones to overtake that knowledge-action boundary (Fig. 1). These products should be conceived as a bespoke modelling framework for the decision-making process, adjusting the development of SDMs to the scope of the problem that arises from the decision context. Here, the decision context is acknowledged as an early step of the decision process aimed to clarify the decision targets, implementation constraints (i.e. timeline, budget, etc.), and role of key stakeholders. On the other side, to develop positive contributions to different stages of the decision process, the SDMs framework needs to fit adequately the challenges arising from the decision context based on a clear definition of the question(s) to be addressed with the models. Spatial products aimed at facilitating decision-making are

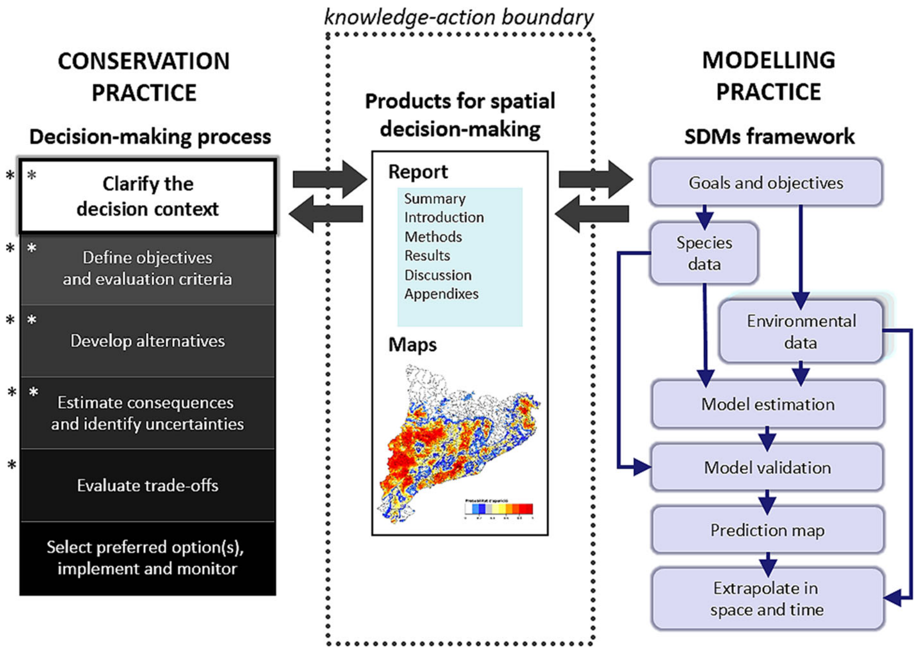

Fig. 1 Information flows between conservation and modelling practices, highlighting the products for spatial decision-making as key translation tools to span the knowledge-action boundary. Theoretical decision-making process showing potential contributions of SDMs via direct assessments (*clear internal asterisk*) or uncertainty assessments (*dark external asterisk*), adapted from Guisan et al. (2013), and SDMs framework adapted from Franklin (2009)

focused on approaching SDMs to the decision context by reporting explicitly all these challenges within the modelling framework in order to feed the decision-making process with clear and useful modelling outcomes.

Against this background, in 2007 we initiated a project called *Mapping priority conservation species in Catalonia* (CARTOBIO) promoted by the Wildlife Agency of the Catalan government, to support spatial data analysis of priority species to enhance conservation management actions. The main objective of the project was to increase species habitat mapping to match particular requirements of pressing conservation problems, posing a timely opportunity to bridge new developments between decision-making and SDMs development. Following the information flow schedule depicted in Fig. 1, the products designed to help spatial decision-making benefited from a number of CARTOBIO learning experiences materialized in successful examples, according to priorities set by the Wildlife Agency. To illustrate the potential application of these products, three best-practice successful examples with significant impact on decisions related to specific conservation problems are summarized below. These examples were chosen to emphasize the three main topics of the information flow between practitioners and modellers (Fig. 1). As many other CARTOBIO applications, these selected examples are characterised by short-term pressing decisions with limited budgets. Examples are also aimed to illustrate different application backgrounds (e.g. conservation planning, environmental payments and human-wildlife conflict management) and decision outcomes (e.g. special protection plans, funding allocation criteria and legal decrees). Specifically, the first is a spatial planning example dealing with the special protection plan of a protected area devoted to the last native population of an endangered tortoise. The example shows the significance of adapting analyses and spatial product definition to the requirements derived from policy document development. The second example involved a spatial prioritisation exercise aimed at the implementation of effective conservation measures targeting the reduction of conflicts between reintroduced brown bears and livestock and the enhancement of the social acceptance of the program to reinforce nearly extinct populations of brown bear in the Pyrenees. The third example shows the translation to a legal decree of a spatial product clearly aligned with specific information requirements from the decision-makers. More specifically, the decree provides spatial prioritisation guidance to articulate compensation payments associated to potential decreases in honey production derived from the presence of bee-eaters. In the next sections, particularities from each example will be used as elements to recognize and discuss the relevant issues potential leading to more effective linkages between practitioners and modellers at the different levels outlined in Fig. 1. The different examples are followed by a more general discussion on the main lessons learnt (linked with the examples) from CARTOBIO applications illustrating how, by refining the products for spatial decision-making, researchers can to better adjust the modelling outcomes to the decision context (Table 1).

Example 1: Identification of habitat corridors to ensure Hermann's tortoise (*Testudo hermanni* subsp. *hermanni*) population connectivity within the Special Protection Plan of the Albera Natural Park

Decision context

The Albera Massif hosts the last native Hermann's tortoise population in the Iberian Peninsula. The upcoming statement of the Albera Natural Park aims at ensuring Hermann's

Table 1 Main lessons learnt for an effective integration of SDMs in a decision-making process

Decision context
Match particular decision targets with pertinent and accurate model objectives
Ensure the feasibility of the model considering the limitations drawn by the decision context (e.g. time or budget constraints, poor species knowledge, etc.)
Clearly identify specific information requirements from the decision-making process
Recognise key roles of other stakeholders, and involve species experts in model development
Modelling framework
Do not deviate from the model objectives informing the decision process
Mobilize relevant available species and environmental information, and engage species experts to interpret adequately available species datasets and relevant environmental predictors
Use contrasted methods with clear and transparent assumptions to increase understanding and trust from decision makers and other stakeholders
Strengthen credibility with a multifaceted model validation based on statistical model-performance measures and expert based criteria, bearing in mind the intended application of the model
Products for spatial decision-making
Describe the modelling framework with clear and accessible/plain language using and adapting good practices from standard protocols (e.g. TRACE)
Identify uncertainties from biological data, environmental predictors, modelling methods using both statistical criteria and ecological realism
Clearly communicate limitations of modelling outcomes, and derive recommendations aimed at the intended use of the spatial products
Align spatial products to specific information requirements by categorizing model outputs into binary or ranked priority maps (e.g. identification of species core areas) and perform complementary analyses (e.g. corridor analyses)
Deliver comprehensive and informative reports embedded with digital maps in standard file formats

tortoise conservation, emphasizing the importance connectivity maintenance between nearby meta-populations. Framed in the drafting of the Special Protection Plan for the Natural Park, decision makers needed spatial information to define formally the core distribution areas of the Hermann's tortoise within the Natural Park, and corridor areas to guarantee interactions between isolated populations. This process encompassed staff from the Wildlife and Natural Parks agencies, as well as species experts, NGOs (Amics de la Tortuga de l'Albera), local administrations and researchers.

Modelling framework

Model objectives involved the development of actual and potential distribution maps, in order to assess Hermann's tortoise core areas and corridor areas, respectively. Available species information included standardized census conducted within the Natural Park (Bertolero 2008). However, preliminary analyses revealed that these censuses omitted significant portions of the species range related with potential suitable corridors outside the protected area. To achieve a more consistent dataset we enriched the 226 records from standardized censuses with 10 pre-processed and complementary telemetry records (see case study 2), covering historical and relevant satellite populations. The ecological requirements of the species were summarized in 22 predictor variables, including climate (12), relief (2), land cover (5), a single vegetation index (NDVI) and log distance to valley

bottoms and burned areas, bounded in a broad study area at 50 × 50 m spatial resolution. Additionally, a spatial contagion variable (or auto-covariable, Augustin et al. 1996) was computed by averaging species frequency within a 1 km buffer around each 50 × 50 cell, in order to examine intrinsic population factors imperative to define species actual core areas. The lack of absence data and the fact that environmental gradients were incompletely surveyed justified the use of the presence-background approach implemented in Maxent, built-in a hierarchical modelling process. That process aimed first to catch climatic suitability areas intended to constrict the environmental background -and improve predictions- of the subsequent models (Phillips et al. 2009). Next steps produced a potential habitat model and an actual habitat model, both based on non-climatic variables, but the latter emphasizing the real current distribution extracted from the spatial contagion variable. All models were trained using Maxent́s default parameters but using only linear and quadratic features, looking for simple models with smooth fitted functions easy to interpret. Models were replicated 5 times in a repeated subsampling procedure designed to evaluate model performance. This procedure randomly assigned 75% of species records to model calibration while keeping the other 25% records to AUC computations. Statistical validation and expert criteria agreed that both actual (AUC = 0.94) and potential (AUC = 0.86) averaged models satisfactorily scored species habitat suitability in the Albera Massif.

Products for spatial decision-making

Hermann's tortoise core distribution areas were defined as highly-suitable areas from the actual habitat suitability map. These areas were drawn by classifying habitat suitability scores in ranked categories. This categorisation was based on two habitat suitability thresholds: suitable areas (used to assess threshold-dependent metrics) and highly-suitable areas (lower limit set as the average habitat suitability values within suitable areas). Corridor areas were assessed using cost-distance analyses weighted by main factors affecting species dispersal abilities, i.e. potential habitat suitability, terrain slopes and human activities. Resulting cost-distance maps measured the cumulative cost to move from any point of the study area to the closest species core area, assuming species maximum dispersal distance of 1600 meters/week (Longepierre et al. 2001). Lastly, potential highly-suitable areas (ranked from potential suitability maps) were included in the cost-distance analysis to identify suitable areas that could be potentially colonized by the species.

The spatial products delivered included digital maps joined to a short executive report. Digital maps pictured Hermann's tortoise actual and potential core distribution areas and connectivity between them as continuous swathes of permeable pixels (Fig. 2a). The embedded report stressed the need to broaden species censuses to cover the species' distribution range in the Albera Massif and, hence, update the analytical outlook for the specie. It was also underlined that model refinement would require information from other major environmental pressures (e.g. illegal collection, high-speed railway lines, etc.). Within the whole process, the analyses of cost-distance were the most affected by the tight decision deadlines, reporting the highest levels of uncertainty derived from the expert-subjective assessment of the permeability of the landscape to species movement (i.e. travel cost) and the poor validation (based only on expert criteria) of the final connectivity maps. Still, spatial products were very welcome and contributed positively to the drafting of the Special Protection Plan, to the extent that researchers were asked to contribute to the chapter devoted to Hermann's tortoise conservation measures.

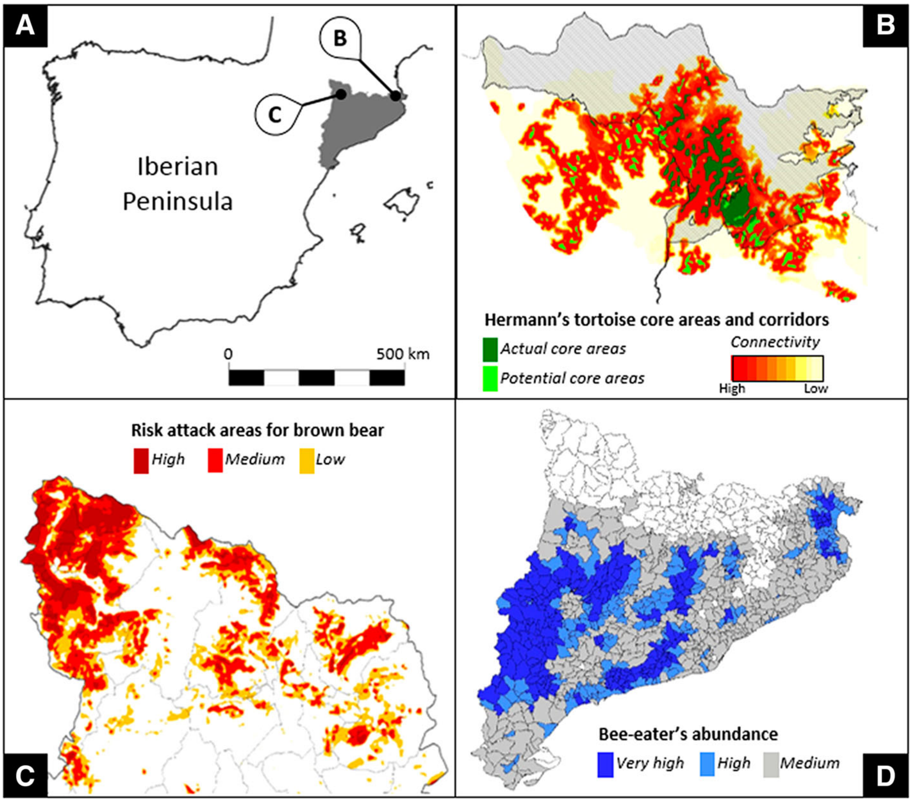

Fig. 2 Examples of digital maps derived from SDMs and appended to products for spatial decision-making. **a** Location of Catalonia (*shaded area* within the Iberian Peninsula) and study areas for **b** and **c** examples. **b** Hermann's tortoise (*Testudo hermanni* subsp. *hermanni*) core areas and corridors to ensure population connectivity within the Special Protection Plan of the Albera Natural Park. **c** Brown bear (*Ursus arctos*) attack risk areas to livestock. **d** Bee-eaters (*Merops apiaster*) abundance map at municipality level to weigh environmental payments established in a legal decree (DMAH 2007) to mitigate the decrease in beehives production due to predation

Example 2: Mapping the risk of brown bear (*Ursus arctos*) attacks on livestock

Decision context

The brown bear went nearly extinct from the Pyrenees at the end of the twentieth century. To prevent extinction, the Catalan government, jointly with other national and regional administrations, promoted an ambitious program to enhance brown bear populations by reintroducing some individuals in the Pyrenees from genetically closer populations at Slovenia. In order to enhance social acceptance, wildlife managers promoted measures to prevent conflicts between brown bear and livestock by installing electrified fences, encouraging the use of dogs to safeguard herds, supporting farming in high mountain (e.g. grouping together larger herds, building facilities to ease shepherd's life, etc.) and compensating livestock farmers for losses caused by brown bear attacks. For the proper implementation of all these measures, decision makers asked for a risk assessment of

brown bear attack to livestock, based on precise spatial information of suitable areas for bears. The decision involved Wildlife Agency practitioners, jointly with species experts, local farmer clusters and administrations, and researchers.

Modelling framework

Seasonal SDMs were targeted in order to examine brown bear distribution across the year, based on the feeding phenology of the species. Available species data from translocated brown bears (1996–2010) included individual telemetry data (seven individuals, $n = 8587$) and monitoring and opportunistic recordings ($n = 1619$). Telemetry data enabled to draw seasonal samples (spring, summer and autumn). Individual telemetry positions were cleaned and bootstrapped following Edrén et al. (2010) to produce 10 replicates per season with equal representation of each individual, totalling a sample size of 55 in spring, 85 in summer, and 60 in autumn, from five individuals (three females and two males; two females removed due to insufficient data). Environmental predictors, circumscribed to the Catalan Pyrenees at 50×50 m spatial resolution, included 16 proxies of food availability (percentage cover of different habitat types) and refuge areas (two for topography, five for human influences and two for forest density). Seasonal models were developed using Maxent method due to its robustness when handling presence-only data and small sample sizes (Wisz et al. 2008). Maxent builds habitat suitability based on the comparison of presence records and background environmental conditions, which makes it particularly adequate for telemetry data that provide no indication of where animals do not occur. Model replications were averaged to produce seasonal habitat suitability maps. To validate model performance, we used threshold-independent (AUC) and threshold-dependent (omission rates and model significance) metrics averaged across seasonal replicates. AUC was computed from seasonal previously excluded telemetry subsamples (AUC-telemetry) and seasonal independent monitoring/opportunistic recordings (AUC-monitoring), while omission rates and model significance were assessed from binary predictions that defined suitable areas as those with habitat suitability above the average 10 percentile fitted values at the training samples. Both AUCs consistently assessed an excellent performance of seasonal SDMs (AUC-telemetry = 0.962–0.971; AUC-monitoring = 0.902–0.941). In parallel, threshold-dependent measures reaffirmed model accuracy, with mean omission rates lower than 0.1 for all seasons (spring 0.047 ± 0.018; summer 0.072 ± 0.023; autumn 0.073 ± 0.031), and always highly significant binomial omission tests ($p < 0.001$, one-tailed).

Products for spatial decision-making

Model outcomes included seasonal habitat suitability maps showing brown bear distribution across the year. However, these maps showed serious limitations to be directly used by decision makers because of the difficulties to distinguish actual or potential areas of occupancy from continuous habitat suitability scores. To tackle this issue, we first highlighted the relative importance of different areas by classifying habitat suitability scores in ranked categories. This categorisation was based on three habitat suitability thresholds: suitable areas, highly-suitable areas (both as defined in Example 1) and optimal areas (lower limit set as the average of habitat suitability scores within highly-suitable areas). Second, hierarchically prioritized seasonal maps were integrated in a single annual map, keeping the maximum seasonal ranked suitability, in which expert knowledge was used to distinguish occupied actual areas from the potential ones (Pearce et al. 2001a). Finally,

low, medium and high-risk areas of brown bear attacks were defined based on ranked suitable, highly-suitable and optimal areas, respectively, and within the actual occupied areas.

Final maps enabled decision makers to identify areas according to their likelihood of being occupied by brown bears in different seasons, and thus, potentially risky for livestock herds (Fig. 2b). The attached report emphasized incomplete individual and gender equity from the datasets, based on only three females and two males of the 8–11 individuals present in the Catalan Pyrenees. Additionally, model improvement suggestions stressed the need to extend the study area (e.g. based on home ranges from telemetry data) beyond political borders.

Example 3: direct payments to beekeepers to compensate for the damage produced by bee-eaters (*Merops apiaster*)

Decision context

Bee-eater is a protected species in Catalonia with a breeding population increasing moderately (+ 3%) over the last 30 years (see http://www.sioc.cat/fitxa.php?sp=MERAPI). However, this increase has affected negatively on honey production, due to the intensification of bee predation and the rising stress on hives. To promote activities compatible with conservation of the bee-eater, the Catalan government compensates the damage on honey production with environmental payments regulated by a legal Decree. This regulation establishes quid-pro-quo payments to beekeepers based on bee-eater's local abundance as well as land apicultural suitability. Hence, bee-eater abundance maps were a key information to tackle this problem. Here, decision was taken to rank municipalities based on apicultural suitability maps, provided by beekeeper clusters, and consistent bee-eater's abundance maps based on bird censuses. The Wildlife Agency guided a decision process that involved NGOs (Catalan Ornithological Institute), beekeeper organizations and researchers.

Modelling framework

To approach a bee-eater abundance map, we used the best available information at that time, i.e. the bee-eater probability of occurrence map from the Catalan breeding bird atlas (CBBA, Estrada et al. 2004). Based on standard and stratified timed censuses that covered approximately 9% (3077 1×1 km squares) of the total area of Catalonia between 1999 and 2002, the CBBA estimated the probability of occurrence of the bee-eater, and other 198 breeding bird species, by means of generalized linear models (GLM) at 1×1 km resolution. Models were trained using species presence-absence reported in standard censuses, and up to 39 environmental variables, including land use (22), human influence (5), climate (3), relief (2) and geography (3). GLM's included as potential predictors all linear and quadratic terms, avoiding all those showed correlations higher than 0.9. Interactions between environmental variables were also included only when their ecological interpretation was highly justified. The most parsimonious models were harvested via the Akaike Information Criterion (AIC), computed from an automatic stepwise model-selection procedure starting from a null model containing the intercept only (Hesterberg et al. 1993). Final models were built adding 3 spatial auto-covariables to the best set of environmental variables previously selected (Augustin et al. 1996). This allowed identifying the best environmental model available given the environmental predictors and

complementing those with information about the spatial structure of the species data (i.e. spatial autocorrelation). It is important to highlight that these GLM models were used as predictive rather than explanatory tools; hence the accuracy of model projections was more important than the significance of a particular ecological term (Legendre and Legendre 1988). Model performance was evaluated based on expert criteria and AUC outcomes from a subsampling procedure that randomly assigned 70% of occurrence values for each species to a calibration data set, and the 30% of remaining occurrences to a test data set (Guisan and Zimmermann 2000), pointing to a very good discrimination capacity for the bee-eater predictions (AUC = 0.85). CBBA probability of occurrence maps included an additional step for removing predicted areas outside species known 10 × 10 km squares distribution range, to ensure that the published occurrence maps corresponded as accurately as possible to real rather than potential distribution maps (Pearce et al. 2001b).

Products for spatial decision-making

Based on CBBA bee-eater probability of occurrence map, we ranked bee-eater abundance at municipality level assuming that the probability of occurrence is a surrogate for abundance and as such is a reliable estimator of a species' relative abundance in each mapping unit. This assumption was strongly supported within the CBBA by consistent population estimates based on species occurrence maps and data from catalan common bird survey (SOCC), and other studies (e.g. Brotons et al. 2007; Robertson and Jarvis 1995). Municipalities were ranked in three abundance categories (medium, high and very high) bounded by (1) the averaged probability of occurrence values within municipalities to set the threshold between medium and high abundances, and (2) averaged probabilities within high abundance municipalities, to define the limit between high and very high species abundance. The spatial products delivered consisted of a short report highlighting the potential to improve (and update) species abundance maps based on monitoring data (SOCC) and dynamic environmental predictors (e.g. remote sensed vegetation indices), coupled with a digital map of municipalities classified in medium, high and very high bee-eater abundance (Fig. 2c). Ultimately, direct payments to beekeepers established in a legal Decree (DMAH 2007) were allocated combining municipalities ranked by bee-eater abundance and the apicultural suitability map.

Making information accessible to decision-makers

Generally, decision-making processes are the meeting-point of multisectoral stakeholders (e.g. government agencies practitioners and decision makers, environmental NGO's, species specialists, researchers, private sectors, etc.), framed within a geographical and cultural background, in which social, economic, scientific and political interests collide (Margules and Pressey 2000). The involvement of key stakeholders along the process ensures the adoption of "good" analytical and consensus solutions, by taking into account constraints and pit-falls related to competing interests (e.g. negative population trends for endangered forest species vs. social consensus to increase forest productivity) (Theobald et al. 2005; MacDonald et al. 2007; Carwardine et al. 2008). From a researcher perspective, a prerequisite to prevent misconceptions is to clearly play an unreservedly role (i.e. provide scientific evidence adjusted to the decision goals). Hence, it is critical to assume that the link between scientific evidence and decision targets is based on the assumption that the

question(s) to be addressed is shaped by the policy or management problem, and thus, not necessarily a top priority in the research agenda.

Here, we discuss the main lessons learnt related to the decision context, the modelling framework, and the products for spatial decision-making (summarized in Table 1) in real world conservation action. For the latter, we emphasize certain requirements that spatial products should fulfil to provide relevant and timely information to build trust and promote utilisation by practitioners, and to improve communication to other stakeholders and targeted audiences.

Decision context

The decision-making process is shaped by the decision context through the definition of explicit objectives and endpoints to address a particular conservation problem, along with budgets, timelines and key stakeholders. The aim of an applied model development is to fit the decision problem at hand with simplified representations of a complex reality. Additionally, modellers should be responsive for the feasibility of the model that should be fit on purpose to the decision context. An early fluid communication with decision-makers helped to clarify these questions and to help identify information requirements. It also contributed toward better recognising the roles of other stakeholder within the decision context.

Another key aspect limiting the feedback between the decision-making process and model development was time and/or budget constraints derived from the decision-making agenda, often responding to urgent need of action. Linking available human resources with a new schedule set by decision-makers required the availability of versatile staff in terms of qualification and scheduling. Having a consolidated yearly budget was a solid incentive to strengthen knowledge transfer in our research group. Nevertheless, difficulties of training and consolidating scientific and technical staff, and an increasingly demanding scientific career for researchers responsible for adding value to knowledge transfer processes often posed a tough challenge for planning the priorities of the research group.

Poor species knowledge or lack of data often represented additional shortcomings to match decision goals. In fact, models are especially suitable tools to make extrapolations based on incomplete data. Even so, incomplete species information became good opportunities for cooperation with species experts' stakeholders (example 1 and 2). Multidisciplinary work was especially effective to complete databases with new biological information, to identify and define relevant environmental predictors, and to validate (by expert opinion) and mainstream (to the extent that experts adopt as their own) model results.

Modelling framework

The first step in any modelling exercise is to clearly formulate the question to be addressed (Franklin 2009; Schmolke et al. 2010). A broad view of the decision context provided us the link between different sources of information, the assumptions made for the model design, and, lastly, to better adjust model outcomes to the type and quality of information required for the decision-making process.

Available data on species occurrence were mobilized and documented, focusing on methodological issues (data types, sample size, life history targets, sampling design, etc.) and fulfilling biodiversity information standards (e.g. Darwin Core: Wieczorek et al. 2012). Information sources were diverse, including specific surveys (example 1), monitoring

programs (example 2 and 3), telemetry data (example 1 and 2) and opportunistic observations (example 2), and mostly designed to meet particular goals far from SDM development. In fact, many sources of information were incomplete (lack of absence data, sampling effort, etc.), and had an inadequate spatio-temporal or environmental coverage (Hirzel and Guisan 2002; Vaughan and Ormerod 2003). Hence, the achievement of consistent data to build SDMs often involved to merge different datasets, seeking the balance between the gain in sample size and the loss in data quality (Chapman 2005) (examples 1 and 2). Data collation and integration implied extra work for data cleaning and standardization, but helped disentangling the potential to meet the challenges posed by the decision context (Rondinini et al. 2006; Hermoso et al. 2013). Experts played an essential role not only to better understand the information from different data sources (i.e. sampling design, survey effort and species counts and other parameters recorded), but also to identify relevant environmental predictors, or their surrogates for modelling species-environment relationships. The availability of reliable and high-resolution environmental databases (climate, relief, land use, habitats and human activities) greatly simplified the definition of environmental predictors (examples 1 and 2). Dealing with environmental predictors collinearities and adjusting them to spatio-temporal scale of the decision were the prior steps to the development of the SDM.

Given the myriad of SDM algorithms (Guisan and Zimmermann 2000; Franklin 2009), we opted for robust methods consistent with available species data and preferably built-in in clear analytical schemes, aimed to make analytical issues more accessible and straightforward, and, thus, trusted by decision makers and other stakeholders. More accessible models included minimizing the number of modelling steps and avoiding the combination of different modelling techniques. Correlative approaches were widely used for different applications, although the more demanding general-purpose statistical methods (e.g. GLMs, GAMs) were generally excluded due to a lack of presence-absence or abundance data recorded in systematic surveys (examples 1 and 2). Even, occasionally the lack of presence-only data justified the use of alternative expert based models (e.g. habitat suitability indices). Nevertheless, presence-only data clearly arised as the best existing data for almost all species, boosting the utilization of techniques based on such data. Among these techniques, Maxent (Phillips et al. 2004, 2006; Phillips and Dudik 2008) emerged as a feasible solution for a wide number of applications because of its flexibility when handling different types of data and responses and its consistent competitive performance in data poor situations (Elith et al. 2006, 2011). Our model implementations benefited from comprehensive research background on the optimization of Maxent for dealing with sample biases (Phillips et al. 2009; Anderson and Gonzalez Jr 2011; Elith et al. 2011; Kramer-Schadt et al. 2013; Yackulic et al. 2013; Fourcade et al. 2014), model parameterization (Warren and Seifert 2011; Merow et al. 2013) and feature types selection (Phillips and Dudik 2008; Elith et al. 2011; Syfert et al. 2013). Another advantage was that Maxent, similarly to other regression methods, correlates species occurrence to selected functionally relevant predictors by fitting response curves using a goodness-of-fit criteria (Phillips et al. 2006; Phillips and Dudik 2008). Moreover, Maxent offers many tuning options for the parameterization of environmental predictors (number of predictors, linearity or non-linearity of the response, additivity or interactions between predictors, etc.), easing to fine-tune predictive or explanatory models to a wider range of applications, and to provide spatial predictions with other informative model outputs.

Model validation enhanced the credibility of model outputs by combining statistical and expert based criteria. Among the different sources of uncertainty arising during model building (Beale and Lennon 2012), model evaluation was explicitly focused on measuring

the accuracy of spatial predictions given the intended application of the model. Statistical criteria included different performance measures frequently used in SDM. In order to get a multifaceted view of the quality of the predictions, models were preferably evaluated by means of threshold-independent and threshold-dependent measures. Debugging treatments of original species data aimed to set aside independent test samples, coming from independent species surveys or from data excluded in model fitting, selected based on the same quality criteria used for the selection of data for model building. Whenever not enough data were available, we used common partitioning methods, based on the sample size and the number of predictors, to split the available species data in two (or more) independent cross-validation subsamples, yielding averaged accuracy estimates among different replicates (Fielding and Bell 1997; Guisan and Zimmermann 2000) (see examples). We used the threshold-independent AUC (Area Under the receiver operating characteristic Curve) (Fielding and Bell 1997; Boyce et al. 2002) as a basic measure of model performance. Despite the limitations of AUC when comparing performance for different species or study areas and its suitability when dealing with presence-only data (Lobo et al. 2008), AUC remains a reliable and widespread measure of model performance (Anderson and Gonzalez Jr 2011). Whenever possible, AUC scores were complemented with threshold-dependent metrics, e.g. omission rates, model significance (Phillips et al. 2006; Anderson and Gonzalez Jr 2011) (example 2). Experts also played a key role in model validation by verifying the ecological accuracy of the environmental response functions and the relative importance of different predictors. Moreover, experts were also asked to evaluate the credibility of spatial predictions using a qualitative scale, based on matching between the spatial patterns predicted by the models and their knowledge on the specieś actual distribution. Ultimately, this feedback enhanced the acceptance of the model outputs and the sufficient degree of belief to justify its further use.

Products for spatial decision-making

Modelling outputs were delivered as informative, short executive reports joined to useful digital maps concomitant to specific information requirements for the decision-making context (see examples). Colourful maps of the predicted distribution of species can be very appealing and suggestive, but they can also be misinterpreted and misused if model objectives and uncertainties are not clearly explained. To minimise these risks, special attention was devoted to reporting uncertainties in each modelling step, to highlight the interpretation and limitations of model outputs, and finally to draw some recommendations to stimulate their use. The executive reports explicitly assessed uncertainties inherent to biological data, environmental predictors, modelling methods and predictions, not only based on statistical criteria, but also on expert criteria and ecological realism of model outcomes (i.e. spatio-temporal significance of species occurrence, correct selection of predictors, accurate description of response curves, fitting of ecologically rational relationships, etc.). Reports were inspired not only by good practices proposed in standard protocols for documenting models (e.g. TRACE: Schmolke et al. 2010), but also strongly influenced by end-user's feedback to articulate the results in clear schemes and accessible and plain language.

Feedback from key stakeholders and practitioners not only allowed to improve executive reports, but also to align spatial products to specific information requirements from the decision context (Laurance et al. 2012). Difficulties to clarify the meaning of predictive maps (habitat suitability, probability of occurrence, species abundance, etc.) and to distinguish actual or potential areas of occupancy from continuous predictions were explicitly

addressed by tuning mapping outputs to better fit decision targets (Guillera-Arroita et al. 2015). For most applications it was necessary to categorize predictions into binary maps (species presence vs. absence or suitable vs. unsuitable habitat) or hierarchically ranked priority maps (ex. suitable, highly suitable and optimal areas) (see examples), to be directly used or to feed further analyses of conservation baselines, corridors (example 1), community assemblages, biodiversity indexes, reserve selection, etc. From the number of methods available to transform model continuous predictions into discrete maps (Liu et al. 2005), we followed previous positive experiences on mapping applications in our conservation arena (Bota et al. 2008; Arcos et al. 2009). These approaches separate, first, species suitable and not suitable areas (or presence-absence areas in terms of the prevalence of the data used in the model development) and, secondly, to meaningfully rank different levels of importance for the species based on the average of predicted values within suitable areas (see examples for more details). Additionally, when it was required to discriminate actual vs. potential distributions, we complemented map tuning with available atlas coarse-scale data and expert knowledge to draw more accurate actual specieś distribution (see examples). Once again, consensus with targeted audiences ensured the acceptance of the final spatial products, and last but not least, the use of standard file formats readable by potential end-users to embed reports and digital maps boosted its dissemination and utility.

Concluding remarks

Supporting decision-making for biodiversity management with scientific information relies on the premise that decision-makers clearly understand the scope of the information received (Addison et al. 2013). But a prerequisite to ensure the usefulness of scientific information is that it is properly fitted and inspired by the decision context (Norton 1998; Schmolke et al. 2010; Guillera-Arroita et al. 2015). Overall, the decision context is built around the concept of structured decision-making process (Gregory and Long 2009). This mechanism is fuelled by multi-stakeholder's contribution, all playing different roles and often rowing in different directions, with decision-makers leading from the cockpit (Knight et al. 2006). Among these actors, researchers assume the role of translators of scientific outcomes matching decision goals and constraints (timeline, budget, data, uncertainty, etc.). Therefore, researchers need to be aware of the decision context and deliberately be included in the decision-making process to the better-fit decision goals. We have identified this step as one of the main bottleneck for effective use of SDMs by practitioners. The availability of data and appropriate methodologies and tools need to be aligned with the constraints imposed by the decision context. One alternative is that researchers acknowledge these constraints and make an effort to fit them into their routines. Another alternative is to develop specific teams of translators with a research background that actively bridge the gap between research, method development and applications. In our opinion, this option is to be favoured and it is cost-effective in the medium and long-term perspectives.

Ecological models represent a valuable tool for supporting environmental decision-making (Starfield 1997; Schmolke et al. 2010). SDMs show the results of predictions in spatially explicit terms, similar to that used in spatial planning, favours its implementation as tools for decision support. But the development of SDMs, as any ecological model, in a decision-making scheme is a challenging process (Schmolke et al. 2010; Addison et al. 2013). If not carefully examined, the decision context may hinder its performance at

different stages, from the ambiguous definition of the modelling goals to the incorrect use of the modelling outputs, through various unforeseen difficulties along the different modelling steps (Guillera-Arroita et al. 2015). Consequently, model formulation requires a clear conceptualization of the decision targets and requirements and, therefore, the integration of critical constraints into the modelling framework (Schmolke et al. 2010). The challenge here is to bridge the gaps between the modelling practice and the decision-making process. This challenge may not entirely depend on the role of scientists in charge of model development, but also on the feedback from other stakeholders. However, our experience is that the early consideration of limitations into model development greatly increases the chances of modelling outcomes being used to guide conservation decisions.

The massive development of biodiversity related information systems, including primary biodiversity data repositories and citizen science online portals, in parallel to increasingly profuse environmental data from remote sensing or other initiatives (e.g. Google Street View), is boosting the growth of SDMs methods and applications (Shanmughavel 2007; Jetz et al. 2012; Rousselet et al. 2013; Brotons 2014; Arts et al. 2015). Critical limitations hampering the effective implementation of SDMs are likely to be reduced while expanding the use of these models to support environmental decision-making (Guisan et al. 2013; Hermoso et al. 2015). Biodiversity data, even for well-known taxa, are largely incomplete and often biased taxonomically, temporally and geographically (Reddy and Dávalos 2003). Assuming that, many authors have pointed out the suitability of models based on presence-only data (Pearce and Boyce 2006; Elith and Leathwick 2007; Phillips et al. 2009), or even other modelling alternatives with scarce data (Elith and Leathwick 2009), to avoid delaying conservation actions for improved knowledge (Grantham et al. 2009). But if real world decisions are to be based on model outcomes, the critical issue is to thoroughly assess model suitability and uncertainties within the context of conservation planning and action (Beale and Lennon 2012). Model evaluation does not only refer to reporting on objective criteria to assess data sources, assumptions and performance requirements inherent to the modelling framework, but also to meet subjective criteria that determine the acceptability of the model within a political and social background (Rykiel 1996; Ludwig et al. 2001; Barry and Elith 2006).

Reporting modelś quality following good practices is a good starting point for more comprehensive and transparent spatial products. Despite there is an overall consensus on the elements that need to be addressed in good modelling practices (Margules and Pressey 2000; Schmolke et al. 2010), they are widely ignored. Some of the reasons behind this are the lack of involvement of key stakeholders, lack of incentives for modellers to follow good practices, and the use of inconsistent terminologies regarding the key steps and issues of the modelling process (Soberón 2004; Schmolke et al. 2010; Addison et al. 2013). In addition, clear documentation is not enough for mainstreaming modelling results if not accompanied by user-useful and user-friendly spatial products (Driver et al. 2003; Reyers et al. 2007). The development of valuable products for spatial decision-making requires an effective communication with decision makers and other stakeholders, especially at early stages of the project (Laurance et al. 2012). Frequent personal contacts (face-to-face meetings, telephone calls, emails) are the best investment to build trust and to better understand particular information requirements from end-users, in order to accurately fine-tune the modelling outcomes to the challenges posed by the decision context (Addison et al. 2013). Thus, products for spatial decision-making can operate as the roller chain to ensure feedback between the decision-making process and the modelling framework, and to enhance communication channels for gaining complicity with practitioners and other

targeted audiences (e.g. land-owners, tourism promotion boards, NGO's, etc.) (Addison et al. 2013; Guisan et al. 2013).

In a rapidly changing and uncertain world, the costs of facing urgent and complex environmental problems with impromptu solutions may imply social and/or environmental irreparable impacts (Mcdonald-Madden et al. 2008; Cook et al. 2010). Ultimately, a simple, rapidly completed plan is better than no plan, but to avoid costly conservation mistakes conservation policies should reinforce linkages between science and both conservation planning and action, for more efficient and transparent decision-making (Knight et al. 2006). This means building capacities by promoting innovative research to impact environmental decisions, which are the substratum for relevant applications in the knowledge-action boundary (Cash et al. 2003; Cook et al. 2013). There are some promising initiatives devoted to reconcile science and policy agendas, both from the perspective of science (e.g. Biodiversity Observation Networks: Scholes et al. 2008; Wetzel et al. 2015) and policy (e.g. Australian National Environmental Research Program: Campbell et al. 2015). Nevertheless, experience-based non-informed decisions are still widely predominant in the realm of conservation practice (Sutherland et al. 2004; Cook et al. 2010). This fact points out the importance for scientists to capitalize opportunities to contribute in multifaceted decision-making processes (Laurance et al. 2012). In the ecological modelling sphere, this means promoting "positive" modelling experiences by properly adjusting the modelling goals to constraints posed by the environmental problems at hand, and by communicating modelling outcomes with clear, accessible and useful information products to aid more rigorous, transparent and reliable environmental decisions.

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